Viability of Sacramento River Winter Run Chinook Salmon

Louis W. Botsford
lwbotsford@ucdavis.edu
and
John G. Brittnacher
jgbrittnacher@ucdavis.edu

Department of Wildlife, Fish, and Conservation Biology
Center for Population Biology
University of California
Davis, CA 95616

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ABSTRACT

The winter run of chinook salmon (*Oncorhynchus tshawytscha*) on the Sacramento River in California (U.S.A.) was the first Pacific salmon stock to be listed under the U.S. Endangered Species Act. We describe some of the characteristics of Pacific salmon populations that require special consideration in viability analysis while developing a model specific to the Sacramento River winter run of chinook salmon. Their anadromous, semelparous life history leads to a special definition of quasi-extinction. Random variability occurs primarily in spawning or early life and is reflected in the cohort replacement rate, the number of future spawners produced by each spawner, a measure consistent with the common practice of characterizing salmon population dynamics in terms of stock-recruitment relationships. We determine the distribution of cohort replacement rates from spawning abundance data and life history information. We then show through simulations that (1) replacing this distribution with a lognormal distribution with the same mean and variance has a negligible effect on extinction rates, but that (2) approximating an indeterminate semelparous life history using a determinate semelparous life history leads to inaccurate estimates of extinction rate. We derive delisting criteria that directly assess the effects of habitat improvement by explicitly including population growth rate (geometric mean cohort replacement rate ≥ 1.0) in addition to abundance ($\geq 10,000$ female spawners). These delisting criteria allow for the uncertainty due to limited accuracy in measuring spawner abundance and the finite number of samples used to estimate population growth rate (estimates must be based on at least 13 years of data, assuming spawner abundance is measured with $< 25\%$ error). Because the probability of extinction will generally be very sensitive to the uncertainty involved in meeting delisting criteria, we recommend that similar uncertainty be accounted for in future recovery criteria for all endangered species.

Introduction

Pacific salmonids (*Oncorhynchus* spp.) are a significant component of the natural heritage of western North America, yet many stocks are at risk of extinction. A recent evaluation of extant, naturally spawning native Pacific salmon stocks identified 214 depleted stocks: 101 at high risk of extinction (i.e., declining or had spawning runs less than 200), 58 at moderate risk (i.e., relatively constant following recent decline), and 54 of special concern for a variety of reasons (Nehlsen et al. 1991). At least 106 additional stocks were known to be extinct. Existing threats and causes of extinction included alteration of flows in spawning rivers, removal of spawning habitat, overfishing in mixed stock fisheries, and hatchery production (Nehlsen et al. 1991; Moyle 1994). Several stocks have now been listed as endangered or threatened under the U.S. Endangered Species Act (ESA), of which the Sacramento River winter run chinook salmon was the first in 1989.

Under the ESA Pacific salmon are delineated by distinct population segments, rather than by species. This view of salmon populations as groups of separate stocks has a long history in Pacific salmon research (Ricker 1972; Thorpe et al. 1981; also see the review in Nehlsen et al.

1991). For purposes of the ESA a distinct population segment is specifically defined as an evolutionary significant unit, which is an interbreeding group of fish that (1) is substantially (but not necessarily completely) reproductively isolated and (2) represents a unique component in the evolutionary legacy of the species (Waples 1991). Using this definition, many races of the six species Pacific salmon species will require specific consideration under the ESA.

It appears the declines in Pacific salmon are primarily due to a combination of deterioration of freshwater habitat, high harvest rates, and negative interactions with other fishes including nonnative hatchery salmon and steelhead (Nehlsen et al. 1991). Restoration efforts will likely involve habitat improvement and harvest reductions, rather than additional hatcheries. Of the declines examined by Nehlsen et al. (1991), most were due to several factors, with 90 percent involving deterioration of habitat, 50 percent involving high harvest, and 53 percent involving negative interactions with other fishes, including nonnative hatchery fish. . They joined others in recommending approaches to reversing the broad decline in these stocks that include greater dependence on habitat restoration and ecosystem function, rather than artificial production through hatcheries (e.g., Healey 1994; Waples 1994). In a review of past performance of the Endangered Species Act, Tear et al (1993) recommended habitat restoration as a necessary component of species recovery in general. Hard et al. (1992) outlined the problems associated with hatchery production of endangered salmonids.

Development of methods for assessing population viability specifically for the anadromous forms of the genus *Oncorhynchus*. will require special consideration of some of their unusual life histories. Although the timing and duration of freshwater and marine phases, as well as the age of maturity of these anadromous fish, vary greatly (Groot & Margolis 1991), all but the steelhead (*Oncorhynchus mykiss*) and sea-run cutthroat trout (*O. clarki*) die after spawning. This indeterminate semelparous life history is more common among plants, but unusual among fishes. Another departure from standard approaches to viability analysis is the fact that all of the population is not subject to the same risk. For example, returning and spawning adults and outmigrating juvenile can be at higher risk at any one time than adults in the ocean. Because of this, parts of a population (e.g., the spawning run every 3 years) can drop to low abundance somewhat independently of the rest of the population. Also, in most cases abundance of only part of the population (i.e., the spawning run) is assessed each year. Because of these factors, special methods of risk assessment will be required to accomplish three basic functions generally associated with recovery of species at risk: (1) assessment of current status, (2) planning strategies for recovery, and (3) establishing delisting criteria. The last purpose, deciding when a species no longer requires special protection, must incorporate fundamental decisions regarding the way in which the risk of extinction is to be reduced, yet it has received little attention in the population dynamics literature. Also, some of the analytical tools needed to address this aspect of the problem, such as accounting for uncertainty in population abundance estimates, have yet to be developed (but see Taylor & Gerrodette [1993], Taylor [1995], Ludwig [1996]).

The winter run is one of four distinct races of chinook salmon in the Sacramento River, each named for the time at which adults enter the river to spawn (Fall, Late Fall, Winter and Spring). Genetic studies suggest that in spite of forced overlap of spawning grounds due to flow alteration and the potential for stocks being cross bred in hatcheries, stocks still appear to be substantially genetically isolated (Fisher 1994; Nielsen et al. 1994). The winter run enters the Sacramento River in January and February, spawns in early summer, and juveniles develop during the summer months, migrating to the ocean the following winter or spring. Historically they spawned in the cool, spring-fed streams on the upper Sacramento, Pit, and McCloud Rivers, Battle Creek and Hat Creek (Fig. 1). Spawning run sizes before the 1870s were estimated from qualitative observations to be in the hundreds of thousands (Stone 1876) and ranged from 180,000 to 300,000 between 1872 and 1896 based on landings in a gill net fishery. Dam construction began to hamper runs in the early 1900s, and completion of the Shasta Dam in the early 1940s sealed off most of the spawning grounds (Fig. 1). The winter run then began to spawn in the waters downstream from Shasta Dam, which happened to be cooled by dam releases at the appropriate time of year (Fisher 1994). Completion of the Red Bluff Diversion Dam (Fig. 1) in 1967 hampered migration to and from the spawning area, but also provided a means of counting almost all spawning adults each year. In recent years the gates of this dam have been open during most of the upstream spawning migration of the winter run to enhance upstream survival. Since migrants are no longer forced to use the counting ladder, this has greatly reduced the precision of this abundance estimate. The current major, correctable factors affecting this stock are degraded spawning and rearing habitat, dams and flow diversions affecting both upstream and downstream migration, pollution from various sources, and ocean harvest.

Reproduction in Pacific salmon is somewhat unusual in that adults die immediately after spawning, and most spawning is typically over two or three ages (cf. Groot & Margolis 1991). This life history pattern is termed indeterminate semelparous (Begon et al. 1990). In a determinate semelparous population spawning at a certain age A, there would be A distinct, independent subpopulations. In indeterminate semelparous species, these subpopulations are not independent. We refer to them here as temporal (as opposed to spatial) subpopulations. The indeterminate semelparity of salmon stocks raises several questions. One, a general life history question, concerns how the relative degree of indeterminancy affects the probability of extinction. A related, more practical question is whether a determinate semelparous life history, which is mathematically and statistically simpler than an indeterminate semelparous life history, can be used to simplify the analysis of extinction probabilities.

Here we develop an approach to the analysis of extinction probabilities specifically for the winter run chinook salmon. In doing so we encounter issues which may be relevant to viability analysis of other Pacific salmonids (and other species, e.g., semelparous plants). We formulate an age structured model of these quasi-semelparous species and evaluate several semelparous approximations. We use this model to determine the current probability of extinction for the winter run of chinook salmon on the Sacramento River, then to develop delisting criteria for that

species. The latter include explicit account of sampling errors and errors in estimation of run size.

A Pacific Salmon Population Model

To assess extinction risk in Pacific salmon, we need a population model that: (1) incorporates Pacific salmon life history characteristics, (2) reflects the type of data typically available, and (3) can be used to compute extinction in a random environment under a variety of conditions. We will confine our interests here to populations for which we can assume that density-dependent effects are not important. This is likely to be the case for endangered salmon populations which are at low abundance because of decreased survival through a phase of their life history such as the spawning run. It would not be the case for populations reduced to low abundance by contraction of the spawning habitat (Botsford 1994).

The information typically available for these stocks is the fraction that spawn at each age, fecundity at age, and some idea of whether the population is increasing or decreasing. Information on fraction spawning at each age is ideally obtained from tagging studies, but could also be estimated from the age distributions of spawners over several years. Although ages of spawning among chinook salmon stocks range from 2 to 8 years, the standard deviations of spawning ages within a stock range from 0.206 to 0.698 years for females, indicating most members of a stock spawn at one or two ages (Healey 1991). For the Sacramento River winter run chinook, we know fecundity and the fraction of a cohort spawning at each age, but we have no direct estimates of survival rate. In a tagging study conducted on three cohorts of winter run chinook, 25% of those tagged fish that returned, returned to spawn as two-year-olds, 67% returned to spawn as three-year-olds, and 8% spawned as four-year-olds (Hallock & Fisher 1985). Virtually all of the two-year-old winter run chinook that spawn are males. We formulate a model of females only, assuming there are always enough males to fertilize all eggs, hence the fraction spawning each year is 89% at age 3 and 11% at age 4. From fish collected at the Coleman National Fish Hatchery over 8 years, the average fecundity is 3,353, but the dependence of fecundity on age is unknown. We assume it is the same for ages 3 and 4.

For populations at levels for which density-dependence is not important, we can describe the deterministic population dynamics as a linear renewal equation in terms of recruitment R_t,

(1)

$$R_t = [R_{t-2}\, p_0\, s_2\, f_2 + R_{t-3}\, p_0\, p_1\, (1 - s_2)\, s_3\, f_3 + R_{t-4}\, p_0\, p_1\, p_2\, (1 - s_2)(1 - s_3)\, s_4\, f_4]$$

where recruitment is defined to occur in the summer, shortly after entering the ocean, p_a is the

fraction surviving from age a to age a+1, s_a is the fraction of the cohort alive at age a that spawns (then dies) at age a, and f_a is fecundity at age a in terms of surviving recruits (cf., Chuma 1981; Kope 1987; Caswell et al. 1984; Hankin & Healey 1986; Kaitala & Getz 1995). This model expresses current recruitment as the result of spawning by each age class present. In the presentation of this model, we include ages 2 through 4; for other Pacific salmon species which also spawn at ages older than 4, the form of additional terms would be similar. This model could equivalently be written in terms of a Leslie matrix. The eventual behavior of this deterministic model is geometric increase at a rate λ, where λ is the positive real solution to the characteristic equation (i.e., an Euler equation),

(2)

$$1 = [\mathbf{8}^{t-2} PO^s 2 \int 2 + \mathbf{8}^{t-3} POP1 (1-s_2) s_3 \int 3 + \mathbf{8}^{t-4} POP1P2 (1-s_2)(1-s_3) s_4 \int 4]$$

and one can determine whether the population is increasing, decreasing or constant from whether lifetime reproduction is respectively greater than, less than or equal to 1.0.

(3)

$$L = [PO^s 2 \int 2 + POP1 (1-s_2) s_3 \int 3 + POP1P2 (1-s_2)(1-s_3) s_4 \int 4]$$

Salmon biologists rarely describe the potential for population growth in terms of λ, rather they keep track of the number of recruits produced per spawner, with recruits and spawners described in directly comparable terms (i.e., both stated in terms of numbers at the same age, usually the age of spawning). This practice arose out of the common use of stock-recruitment descriptions of the density-dependence in salmonid reproduction and recruitment (e.g., Ricker 1954; Larkin 1988).

Formulation of a model that will be useful in estimating probabilities of extinction requires an accurate description of the dominant sources of random interannual variability in population dynamics. Although some endangered Pacific salmon populations are at low enough abundance that discrete demographic events must be explicitly treated as random (e.g., the Snake River sockeye), here we will assume high enough abundance that demographic stochasticity is not important. The main source of random variability in Pacific salmon populations is the random environment in the freshwater phase associated with reproduction. Natural and anthropogenic variability in river flows have a large effect on both upstream and downstream migration (e.g., Kjelson & Brandes [1989] for Sacramento River fall run chinook), and during these migrations salmon will have greater exposure to a variety of other risks. There is some evidence that even the marine environmental influences occur at the end of this period, at the time of ocean entry (e.g., Kope & Botsford [1990] for Sacramento River fall run chinook; Pearcy [1992] for other

Pacific salmonids). An exception to this would be the effect of El Niño events, which have their greatest effect on growth and survival of adults at any age (e.g., Johnson 1988).

To introduce random variability in the reproductive / recruitment phase into this model, we first rewrite equation (1) so that it includes only terms whose values are known. Typically, we do not know survivals p_a and spawning probabilities s_a, but we know the fraction spawning at each age. We define the total number of spawners per recruit as
(4),

$$P = p_0 s_2 + p_0 p_1 (1 - s_2) s_3 + p_0 p_1 p_2 (1 - s_2)(1 - s_3) s_4$$

then normalize each term in equation (1) by dividing by P, to form
(5)

$$\sigma_2 = \frac{p_0 s_2}{P} ; \sigma_3 = \frac{p_0 p_1 (1 - s_2) s_3}{P} ; \sigma_4 = \frac{p_0 p_1 p_2 (1 - s_2)(1 - s_3) s_4}{P}$$

using these in equation (1) leads to
(6)

$$R_t = [R_{t-2} \sigma_2 f_2 + R_{t-3} \sigma_3 f_3 + R_{t-4} \sigma_4 f_4] P$$

If fecundity is the same at each age, we can call it f , and factor it out of the term in brackets (if not, it can be incorporated in the definition of the s's). We then add a time-varying factor that incorporates the factor needed to normalize the coefficients (i.e., P) and fecundity (f), and reflects the influence of the time-varying environment between the time of upstream migration (i.e., the adult census at Red Bluff Diversion Dam) and the first month or so of ocean life, by replacing Pf with E_t. The resulting model is:
(7)

$$R_t = [R_{t-2} \sigma_2 + R_{t-3} \sigma_3 + R_{t-4} \sigma_4] E_t$$

The factor E_t is essentially a time-varying version of lifetime reproduction L from the deterministic model. If it had a constant value of 1.0, population abundance would remain constant. Because it reflects the relative amount that a cohort recruited at time t contributes to future recruitment, we refer to it as the cohort replacement rate.

To project probabilities of extinction, we must describe the distribution of the random variability E_t. For populations for which a time series of spawning counts is available and the age distribution of spawning is known, the distribution of E_t can be determined empirically. For the winter run chinook, estimates of spawning run abundance, which we will call S_t, are available from a counting station at the Red Bluff Diversion Dam (Figs. 1, 2). The term in brackets in equation (7) is the number of spawners in year t divided by P. Substituting $R_t=(S_t /P) E_t$ for each recruitment in that expression yields an expression for the number of spawners in terms of past spawners,

(8)

$$S_t = \sigma_2 E_{t-2} S_{t-2} + \sigma_3 E_{t-3} S_{t-3} + \sigma_4 E_{t-4} S_{t-4}$$

This expression can be fit to the spawner count data in several ways. One approach is to use the age structure of spawners described above: $\sigma_2 =0.25$, $\sigma_3 =0.67$ and $\sigma_4=0.08$ and determine the values of cohort replacement rates that minimize the squared differences between logarithms of spawning abundance from the model and the estimates of spawning run abundance. The result is shown in Fig. 2. A problem associated with this estimation procedure is the tendency for occasional negative values of cohort replacement rates. These can be prevented by constraining estimated values to be greater than a small, positive value, but the value chosen influences the subsequent statistical characterization of cohort replacement rate. If the constrained values of cohort replacement rate are omitted from computation of the geometric mean of the cohort replacement rates, they lead to a positive bias, and if included, they bias the estimate of the geometric mean by an amount dependent on the value chosen as a constraint. The mean ln(cohort replacement rate) not including values at the constraint was -0.326, the standard deviation was 1.031 and the constraint (cohort replacement rate=0.066) was incurred 5 times.

A second approach is to assume values of σ_2, σ_3,and σ_4 corresponding to a determinate semelparous population (i.e., $\sigma_2 =0.0$, $\sigma_3 =1.0$, $\sigma_4 =0.0$). This approach guarantees positive values of cohort replacement rates and produces an exact fit to the spawning run abundance data. We used the distribution of cohort replacement rates from this approach in subsequent calculations (Fig. 3). The mean and variance of this distribution are -0.631 and 1.059 respectively, and it differs little from the distribution obtained using the other approach, except for the constrained values. This approach to estimation enables one to obtain a distribution of cohort replacement rates that is close to the actual in a situation in which the actual distribution cannot be recovered from spawning abundance data (see Discussion for further details). There was no correlation between values of cohort replacement rate in different years, so we were able to simply choose independent values in simulations.

Analysis of extinction probabilities for Pacific salmon will require a specific definition of extinction. For mathematical and biological reasons we use a quasi-extinction approach (Ginzburg et al. 1982). Quasi-extinction is defined to occur when a population falls below a

specified level. The mathematical reason for using this approach is that the random matrix model as structured here will not reach an abundance of zero. Biologically, a quasi-extinction approach makes sense because it can reflect existing population mechanisms that dramatically increase population jeopardy at low numbers. These mechanisms are Allee effects, in which recruitment drops to near zero before spawner abundance declines to zero (Allee 1931; Dennis 1989).   In Pacific salmon, the most likely Allee effects would be failure to find mates at low abundance and predator saturation during the downstream migration or at ocean entry (e.g., Peterman 1987, and references therein).

Pacific salmon differ from most other populations in that only part of the population (i.e., spawners) is at risk of falling below a quasi-extinction threshold at any one time. For Pacific salmon, therefore, only those currently spawning should be compared to a threshold level at any one time. The number we compare to the threshold level is the current number of spawners, i.e., the abundance of the spawning run, not the total number in the population. We chose a value of 100 females as the quasi-extinction level below which we defined complete failure of a spawning run to occur. In an attempt to detect depensatory effects at low population levels of a number of fish species, Myers et al. 1995 found depensation in only a few. Among the few were several salmon stocks, and in the most convincing case depensation occurred at 100 females.

Defining extinction to depend on spawning runs dropping below a specific level, presents a problem when trying to combine the effects of spawners going extinct in various years into a definition of extinction of the whole population. A reasonable approach is to define population extinction to have occurred when all of the A temporal subpopulations have gone extinct, where A is the age at which most individuals spawn. Because Pacific salmon populations are indeterminate semelparous, not determinate semelparous, this approach incurs a potential problem: by the time the last subpopulation has dropped below the extinction level, one or more of the other temporal subpopulations may have increased to a level such that it is no longer below the extinct level. The likelihood of this obviously depends on how each individual extinction of a spawning run is treated. We chose to set the reproduction by a spawning run to zero each time a spawning run dropped below the extinction level.

An interesting consequence, of relevance to Pacific salmon in general, is that on the time scales commonly considered in computing extinction probabilities (i.e., less than 100 years), once a temporal subpopulation has become "extinct" (i.e., not spawned at the age of maximum reproduction), it appears to increase from zero to above the extinct level within 100 years only very rarely. We demonstrated this for the spawning age distribution of the winter run chinook, as well as for other distributions in general, by simulating populations that all had the same probability of extinction (set by adjusting the geometric mean of the cohort replacement rates). The number of cases in which cohorts that were counted as extinct and set to zero subsequently rose to above the extinction level was always less than 2 percent (Table 1). Because of this, in computing probabilities of extinction for winter run chinook salmon, most of whom spawn at age

3, we needed only to keep track of the time at which the third temporal subpopulation went below the quasi-extinction threshold.

With extinction defined, we turn to evaluating the sensitivity of extinction to the values of spawning distribution used and the distribution of environmental variability, cohort replacement rate. We evaluate these aspects for mean values of cohort replacement rate in the range that will be of most interest to analysts. In work with endangered species, neither a rapidly decreasing population in danger of imminent extinction, nor an increasing population in no danger of extinction will typically be the focus of this kind of analysis. We therefore explore behavior for geometric mean values of cohort replacement rate near 1.0.

The first question we asked was whether we could approximate the indeterminate semelparous population with a determinate semelparous population that spawned at the age of maximum spawning. It would be mathematically and numerically much simpler to determine probabilities of extinction of determinant semelparous populations, because of the lack of age structure and the independence of temporal subpopulations (e.g., using the results of Lewontin and Cohen 1969). We tested this by simulating populations with different age structures, starting from an initial abundance of 10,000. We chose a distribution of cohort replacement rates with mean in logarithms of -0.2 and standard deviation in logarithms of 1.0 so that we could easily see differences within a reasonable time period. The results show that extinction probabilities for Pacific salmonids are sensitive to the distribution of spawning over age. Probabilities of extinction for determinate semelparous populations increase much more rapidly with time than populations that have even the slightest number of individuals spawning at other ages (Fig. 4). In addition to the importance this result has in comparing life histories, it has a disappointing effect on prospects for analysis. Approximating indeterminate semelparous populations with determinate semelparous populations does not appear feasible.

The next question addressed was how sensitive the probabilities of extinction were to the actual shape of the distribution of cohort replacement rates. We wanted to know whether in simulating this population we needed to sample from the distribution of cohort replacement rates indicated in Fig. 3, or we could simply use a Gaussian distribution of ln cohort replacement rate with the same mean and standard deviation of ln (cohort replacement rate). The distribution of ln cohort replacement rates (Fig. 3) is not Gaussian using the logarithmic test appropriate for data which may not match in the tails (p<.001; Zar 1984). To test whether we could use a Gaussian distribution, we compared extinction probabilities from simulated populations with the cohort replacement rates in Fig. 3 to those obtained from simulations using a Gaussian distribution with the same mean and standard deviation. The results indicated that a Gaussian distribution gives probabilities of extinction very close to the values obtained with the estimated distribution. Thus, in this case, probabilities of extinction appear to be relatively insensitive to the distribution of randomness in environmental effects about any specified mean near 1.0. For the following analysis we used Gaussian distributions of ln cohort replacement rates.

Viability and Recovery of Winter Run Chinook

We can now apply this model of extinction of a salmon population to the practical problems associated with recovery of the winter run chinook stock. Of the three functions that viability modeling can fulfill, (1) assessment of the current probability of extinction, (2) formulation of delisting criteria, and (3) evaluation of strategies for recovery, the first is trivial for the winter run chinook. Here we focus on the second, and make only qualitative comments regarding the third. From the geometric decline in spawning abundance in Fig. 2, the computation involved in the first task is merely a formality for this population. Based on the distribution of female spawning over age, and the distribution of cohort replacement rate estimated above, the probability of the winter run chinook salmon going extinct soon is essentially 1.0.

Delisting Criteria

The delisting criteria are a complete, quantitative specification of the conditions that the listed stock must meet to be considered to have recovered to the point that it is no longer likely to be in immediate danger of extinction in the near future. Quantitative specification of the danger of extinction requires definition of the time period and probability level we will consider safe from extinction. For the winter run chinook, we decided on a probability near 0.1 over a period of 50 years. This is less conservative than criteria used for some other species, but is considered safe because (1) we specifically account for uncertainty in estimates of population parameters when delisting and (2) this population is likely to be closely monitored, not just brought to the delisting level, then assumed recovered, without further attention.

The choice of conditions to be required for delisting is a critical one. In most recovery plans for the U.S. ESA, only population abundance has been specified. However, specification of abundance only does not completely reflect future prospects for population abundance and extinction. Rather some specification of population growth rate is required. This is especially important for salmon stocks for a couple of reasons. First, salmon stocks can be increased to high abundance fairly quickly and easily through artificial propagation. It would not make sense to specify a delisting abundance that could easily be met by construction of a temporary hatchery. Second, natural population growth rate is an integrated reflection of the various factors affecting habitat quality. Hence, including it in delisting criteria specifies general habitat improvement as suggested for salmonid stocks (Nehlsen et al. 1991; Healy 1994; Waples 1994), as well as for endangered species in general (Tear et al. 1993).

Construction of the delisting criteria thus requires choice of the population growth rate and abundance to be specified. Here we use the geometric mean of cohort replacement rate as the definition of population growth rate. One could choose the values of population growth rate and abundance required for delisting based on the tradeoffs involved in their combined effects on

probability of extinction (Fig. 5). For the definitions used here, a decline in the mean of the natural logarithm of cohort replacement rates of 0.2 requires an increase in specified initial abundance of roughly an order of magnitude to maintain the same probability of extinction. While this figure demonstrates the trade-off between growth rate and initial population abundance, we did not use it directly to choose an acceptable combination because it does not include the effects of estimation and sampling errors on probability of extinction. We chose a population growth rate of ln(cohort replacement rate)=0.0 somewhat arbitrarily because it corresponds to a constant deterministic population. We then chose a level of spawning abundance to satisfy the condition on probability of extinction (i.e., less than 0.1 over 50 years). A spawning abundance of 10,000 females yields a probability of extinction near 0.1 when sampling and estimation error are accounted for. We use that spawning abundance in the following calculations to demonstrate how accounting for sampling and estimation error increase the corresponding probability of extinction from the value less than 0.01 shown in Fig. 5 to near 0.1.

Sampling Error

Direct use of the relationships in Fig. 5 is limited by the fact that at the time of possible delisting, we would not know the geometric mean of cohort replacement rate, but rather would have to estimate it from recently observed values of spawning abundance. Because that estimation would involve some error, we must include the effects of that imprecision on the resulting probability of extinction. To include the error in the estimate of cohort replacement rate, we write the probability of extinction as the probabilities of extinction for each possible value of cohort replacement rate, summed over the probability of occurrence of each value,

(9)

$$P[extinction] = \sum_{\overline{E}} P[extinction|\overline{E}]P[\overline{E}|\hat{E}],$$

where $\overline{E}$ = the geometric mean of cohort replacement rate and $\hat{E}$ = the estimate of the geometric mean of cohort replacement rate. To investigate the effects of sampling variability on the probability of extinction, we note that the effect of many estimates of $\overline{\overline{E}}$ of 1.0 would be a distribution of true values of $\overline{E}$ equal to $P[\hat{E}|\overline{E}]$ with $\overline{\overline{E}}$ =1.0, so that we can represent $P[\hat{E}|\overline{E}]$ with $P[\hat{E}|\overline{E}=1.0]$ in equation (9). One could estimate the probability distribution of the estimate $P[\hat{E}|\overline{E}=1.0]$ from a description of the errors incurred in the estimation of cohort replacement rates described above.

However, the relative insensitivity of the probability of extinction to the distribution of cohort replacement rates and the age distribution used to estimate the distribution of cohort

replacement rates (including a determinant semelparous distribution) suggest a simpler, approximate approach.   Estimation of the geometric mean of cohort replacement rate in the semelparous case can be accomplished by estimating the mean of the logarithm of the cohort replacement rates, an estimate whose sampling statistics are well known.   The variance of an estimate of a mean is the variance of the samples divided by the number of samples, and the distribution of errors is Gaussian if the variance is known, and Student-t if it is not. Since future habitat improvement will be likely to lead to less variability in the environment, we have made the conservative assumption that the variance in the samples will be the same as the current variance and have not estimated it. Thus the variance in the estimate of the mean of the logarithm of the cohort replacement rates is the variance in ln(cohort replacement rate) divided by the number of samples used to estimate the mean of ln(cohort replacement rate).

To estimate the effect of varying sample size on probability of extinction, we simulated populations with an initial abundance of 10,000, the baseline spawning distribution and the estimated standard deviation of cohort replacement rates. For each sample size, we computed the standard error as the standard deviation divided by the square root of the sample size, then the probability of extinction for every possible estimated value in that distribution, assuming a mean ln(cohort replacement rate) = 0.0. We summed over all of these as indicated by equation (9). The results show the dramatic effect of sample size on the probability of extinction (Fig. 6). At least 7 samples are required to reach the range of probabilities less than 0.1. Note that because an estimate of cohort replacement rate requires 4 years of data, an indication of n samples in this figure would requires n+4 years of spawning abundance data to estimate the required number of values of cohort replacement rate.

Measurement Error

These results assume that spawning abundance is known exactly, whereas for most endangered salmonids, estimating spawning abundance will involve an error, which we term measurement error here. For example, for the winter run chinook, spawning runs were known with negligible error from 1967 through 1985 from counts taken at the Red Bluff diversion Dam. Since 1985, however, the gates of that dam have been open during the early portion of the migration of winter run, hence spawning counts are available only during the last 13 weeks of the 35 week run and abundance must be estimated with associated error.

We can determine the impact of measurement error on our estimate of the geometric mean of cohort replacement rate by approximating it with the value that would correspond to a determinate semelparous population. If all individuals reproduced at the same age, $E_t = N_t/N_{t-3}$. Since most methods of population estimation have a certain percentage error, errors in logarithms of cohort replacement rate would be additive, resulting in a variance in $\ln(E_t)$ of $2\sigma_M2$, where σ_M is the variance of the measurement error involved in estimating the logarithm of spawning abundance. The impact of this error on the estimation of extinction probabilities associated with

estimating ln(cohort replacement rate) can be determined by simply adding $2\sigma_M2$ to the error-free environmental variance (assuming measurement error is independent of environmental variability). The resulting relationship can be displayed as extinction rate in terms of both sample size and estimation error (Fig. 7). From these results one can choose the combination of sample sizes and estimation errors required for recovery.

For the winter run chinook salmon, for example, we chose an estimation error of 25 percent, which is achievable in many population estimates in general, and corresponds to a requirement of 9 samples. Because each estimate of cohort replacement rate requires 4 years of data, this would correspond to 13 years of escapement. An estimation error of 25 percent requires that a new method of estimating spawner abundance be implemented. Note, however, that we could have used the current method of estimating spawner abundance and required additional samples. The precision of the current method can be estimated from a regression of complete counts (weeks 49-32) from 1967 to 1985 on counts from the current counting period (weeks 20-32). A regression of natural logarithms with slope 1.0 yields a mean-squared-error of 0.831, which corresponds to an approximate percentage error of a little over 100 percent (the one standard deviation range is from 0.44 to 2.22 times the estimate). From Fig. 7, continued use of those counts would require about 18 samples.

From these considerations delisting criteria were chosen for the winter run chinook salmon that specified population growth rate in addition to abundance, and accounted for sampling as well as estimation error. The abundance level chosen was 10,000 female spawners per run, and the geometric mean cohort replacement rate was chosen to be 1.0. The number of samples of spawning abundance was chosen to be 13 (i.e., 9 estimates of cohort replacement rate), assuming an estimate of spawning abundance with error less than 25 percent. If that error could not be achieved, the number of samples was specified to increase by one sample for every 10 percent error greater than 25 percent. These are not the only choices that yield a probability of extinction over 50 years of 0.1. The combinations of number of years for which estimates of spawning abundance are required, the spawning abundance, and standard error (in logarithms) of measurement error are shown in Fig. 8. Note that specifying higher mean abundance in spawning runs would require fewer years of sampling to obtain an adequate estimate of population growth rate. On the other hand, mean abundances less than 10,000 quickly begins to require a prohibitive number of samples.

Discussion

These results were obtained in the formulation of a model for assessing risk specifically for the winter run of chinook salmon in the Sacramento River, however some of them apply to anadromous Pacific salmon in general, while others have important implications for endangered species in general.

Winter Run Chinook

While the model developed for the winter race of chinook salmon on the Sacramento River may provide some basis for the analysis of population viability of Pacific salmon in general, some of the characteristics of this stock are unique. Because the geometric decline in abundance indicates low constant survival, rather than density-dependence and a rapid decline in a limiting resource such as the amount of spawning area, the model developed does not include density-dependence. It would, therefore, not apply to populations currently at low abundance due to reduction in spawning area, for example. Emlen (1995) included density-dependence in recruitment in a model of the spring run of chinook salmon on the Snake River and found that while abundance depended on a parameter reflecting carrying capacity, extinction depended primarily on the density-independent parameter.

Because the winter run can be considered to be isolated from the other major runs and there is currently only one spawning location for this stock, the model developed was for a single population. Some Pacific salmon stocks, in particular those that are not mainstem spawners, will require metapopulation models with straying between subpopulations. A third characteristic of winter run that is somewhat special is the availability of a time series of spawning abundance. For some stocks, such as most coastal coho salmon stocks in California, there will be only aggregate catch data from the fishery, while for others, such as some spring run and summer run chinook salmon on the Columbia River and the Snake River the information on age structure and harvest necessary for complete run reconstruction will be available.

Most of the results obtained here employ the life history characteristics of winter run chinook, hence apply directly only to a stock with that spawning distribution. The winter run tends to be closer to determinant semelparous than the other Sacramento River runs (Fisher 1994), and probably most chinook stocks (Hankin & Healey 1986; Healy 1991). The shape of this age distribution is in part due to harvesting. Harvest rates in the 1970s and 1980s are not known but there are recent indications that current rates, which would be similar, are substantial. The values of s_a may change in the future if harvest rates are decreased. We have in several instances evaluated the sensitivity to specific parameter values, however prudent use of this approach will require evaluation of specific parameter values. For clarity, we did not present the age-structured model in terms of completely general sums over an arbitrary number of age classes, but the extensions are straightforward.

Some of the specific numerical values chosen in the viability analysis of the winter run chinook deserve comment. That the time period (50 years) and the threshold extinction probability (0.1) are respectively on the low and high sides of the ranges of commonly used values may appear risky. However there are several other aspects of the formulation that tend to be conservative. The most significant is the inclusion of the effects of uncertainty in estimation of parameters for delisting. From the low probabilities of extinction corresponding to high numbers of samples on Fig. 6, one can see that if we ignored the effects of uncertainty, the stated probability of extinction would be less than .01. Also, we assume that the winter run chinook salmon will be a closely monitored population The presence of three other salmon stocks in this system, one of which has been proposed for listing under the ESA, another listed species, several other proposed species, and the central importance of these waters to California's agricultural economy imply this population will be closely watched.

Because there have been some changes in flow management since the mid-1980s, we were concerned that the samples of cohort replacement rate since then might have inordinately influenced our estimate of natural variability. However, there was no significant difference between estimates of the variance of cohort replacement rates for the periods before and after 1983.

One of the ongoing and important aspects of viability analysis of this winter run chinook not described here is use of this model to formulate recovery strategies. Recovery strategies require determination of the effects on cohort replacement rate of controllable influences (e.g., river flows, harvest) and uncontrollable influences (e.g., precipitation, ocean conditions). These can be determined either by assessing covariability between cohort replacement rates and environmental time series or by incorporating environmental time series directly in the estimation of cohort replacement rate. Recovery strategies can then be formulated from the combined effects of these various influences and consideration of extraneous factors. The fact that extraneous factors for one salmonid stock may involve other salmonid stocks linked either through migration and a metapopulation structure, a common harvest, or a common source of water for dam releases may lead to consideration of several stocks at once. Recovery strategies require consideration of the combination of actions that will lead to two levels of population growth, one during the recovery phase and a second during the recovered, sustained population phase. Use of artificial rearing may be considered in the former. Uncertainty in the estimation of the effects of various factors on population growth rate suggest close monitoring and adaptive responses during the increasing phase.

It is difficult to estimate the time to recovery for this species. The time required for the population to reach a level at which it could be considered for delisting will depend on the specific actions taken to reach a female spawning abundance of 10,000. Beyond that, the time required to accumulate enough samples for delisting will be the time required to obtain 9 samples of cohort replacement rate, 13 years. Simulation results indicate that a population that should qualify for

delisting, i.e. one for which female abundance is 10,000 and the mean ln(cohort replacement rate) is 1.0, will satisfy the criteria in the first possible year more than 60 % of the time.

Pacific Salmon

We have assumed that in a population of anadromous Pacific salmon, the individuals currently spawning are in greater jeopardy of falling below a critically dangerous level than the rest of the population, hence we use spawning abundance as the fundamental unit to be tested against a quasi-extinction criteria, rather than using total abundance, as is done in most models of population viability. A primary reason for this is that most Allee effects considered for Pacific salmon depend on numbers in a spawning run as opposed to total numbers in the population. As a consequence of these, one cannot take the typical quasi-extinction approach (Ginzburg, et al. 1983) of computing the probability of total abundance being less that a threshold, but rather must compute the probability of a segment of the population (current spawners) being below a threshold. The fact that an Allee effect can depend on abundance of only part of a population is not completely unique to Pacific salmon. Although rarely mentioned, it would be true of any population in which, for example, failure to find a mate is the purported Allee mechanism underlying the threshold (see Cisneros-Mata et al. 1997 for some of the implications).

Recent findings indicate shifts in atmospheric and oceanographic regimes may have a dramatic impact on salmon in the marine phase of their lives. For example, an intensification and shift in the position of the Aleutian low pressure zone in the mid 1970s apparently led to a fundamental shift in the physical state of the north Pacific (Miller et al. 1994), an increase in salmon stocks in the Gulf of Alaska, and may possibly have contributed to a decline in stocks in the contiguous U.S. (Pearcy 1992; Beamish 1993; Hare & Francis 1995). The possibility of such regime shifts in marine salmonid habitat on decadal time scales has important implications for recovery of endangered salmon. Formulation of recovery strategies will require the ability to differentiate between natural and anthropogenic causes in order to recommend changes in the latter (e.g., the last dams on the upper Snake River where the endangered spring/summer chinook salmon spawn, were completed in the mid 1970s, about the same time as the regime shift). Also, changes in marine survival on these decadal and shorter time scales may need to be considered as another source of random variability in viability analysis. To the extent that they are similar to El Niño events, they would tend to add variability in adult survival (Johnson 1988).

The accuracy of estimating cohort replacement rates from time series of spawning abundance of Pacific salmon will depend on the age structure (i.e., the values of σ_a), as well as measurement and structural errors in the data. The estimation procedure is essentially a deconvolution of the age-aggregated spawning data, hence the numerical properties of deconvolution (Kope and Botsford 1988) can be used to assess these dependencies. Declining age structures (i.e., $\sigma_4 < \sigma_3 < \sigma_2$) will lead to better estimates of cohort replacement rates than those with partial recruitment of younger age classes (i.e., $\sigma_2 < \sigma_3$). The age structure used here to

estimate the cohort replacement rates is particularly error prone, but others may not be. Measurement errors for the direct counts available for winter run chinook are probably quite small, and will probably be greater where other methods are used. Structural errors (i.e., temporal variability in values of σ_a) could be large in Pacific salmon. The age of maturity can vary from year to year in Pacific salmon (e.g., Peterman 1985). Some forms of structural variability such as varying harvest rates may be known for some species, hence can be used to improve estimates. While these problems may affect the precision of estimates of individual values of cohort replacement rates, because of the relative insensitivity of probabilities of extinction to the exact form of the distribution of cohort replacement rates, we do not expect they influenced the results obtained here.

The large difference in probabilities of extinction between the determinate and indeterminate semelparous models (Fig. 4) implies there may be a broad range of extinction risk among Pacific salmon with different life histories. Cognizance of this fact provides a rationale for organizing and justifying different levels of protection for the various stocks. This result also implies that the effect of harvesting on the age structure of a Pacific salmon, which is to skew the age distribution to fewer, lower ages, will be to increase the risk of extinction. This result for indeterminant semelparous populations is consistent with the idea in life history theory that distribution of reproduction over several ages leads to greater persistence in semelparous populations (e.g., Murphy 1967; Stearns 1992). Hankin & Healy (1986) obtained a related, , but different result. They showed that the growth rate of deterministic, density-dependent salmon populations became negative at lower harvest rate in populations with spawning over a broad range of ages than in populations with spawning over a narrow range of ages. That result is due to a differential effect of harvest rate on reproduction per individual, which we hold constant in Fig. 4.

The fact that a determinate semelparous model fails to approximate an indeterminate semelparous model that differs only marginally is also disappointing from a methodological point of view. Being able to approximate an indeterminate semelparous population with a determinate semelparous population would make a variety of simple approaches useful (e.g., Lewontin & Cohen 1969). Furthermore, the indeterminate semelparous life history of Pacific salmon casts doubt on the applicability of some otherwise useful general results (e.g., expressions for the distribution of abundance of age structured populations [Tuljapurkar 1982] and the consequent diffusion approximation [Lande & Orzack 1988] assume iteroparous populations). Analytical methods which assume either determinate semelparous or strictly iteroparous populations should be carefully evaluated before use in the gray area of indeterminate semelparous populations. Viewing these indeterminate semelparous populations as temporal metapopulations with marginal "dispersal" between them is probably a useful metaphor.

Endangered Species

The importance of explicitly including effects of uncertainty in parameter estimates in projections of probability of extinction is becoming more widely recognized (Botsford 1994, Taylor 1995, Ludwig 1996). Here, the dramatic difference between probabilities of extinction computed from an estimated value of population growth rate and a known population growth rate (e.g., extinction probabilities for few samples vs. the probability for 1,000 samples in Fig. 6) implies that similar uncertainties should be explicitly accounted for in delisting criteria for other species. Estimates of extinction probability that do not account for uncertainty can substantially under estimate probability of extinction (see Ludwig 1996, 1997 for other examples). The sensitivity of extinction rate to uncertainty in the estimated value of mean population growth rate results from the fact that the probability of extinction depends sharply on the mean population growth rate (i.e., in the case addressed here $dP[E]/dE \ll -1$ near ln(cohort replacement rate)=0.0). Therefore any uncertainty in the value of average population growth rate increases the probability of extinction dramatically. This result is not specific to the use of cohort replacement rate, but would also be true for other measures of population growth rate such as the rate of geometric increase, l. Accounting for such uncertainties is not without problems, both conceptual and real. In computing the impact of uncertainty in the mean value of ln(cohort replacement rate) on the probability of extinction, we needed the conditional distribution of actual values of ln(cohort replacement rate) given the estimated value of 1.0, which is unknown. Because it is unknown, we used the conditional distribution of estimates given a true value of 1.0. Because this is one of the terms in the desired conditional distribution expressed using Bayes theorem, this is a reasonable approximation, especially considering that there is no prior knowledge of the mean value of ln(cohort replacement rate) under current conditions.

The effects of uncertainty on estimates of extinction probability can be described in several ways (see Ludwig 1996 for a discussion). Here we characterize these effects directly as an increase in the probability of extinction over the "inherent" probability of extinction so that we can we can use this measure to determine the required number of samples and estimation error. This is justified because the uncertainty in estimation is merely an extension of the uncertainty implied in our usual expression of the "inherent" probability of extinction of a species. The "inherent" probability of extinction is an explicit acknowledgment of uncertainty; if we could predict the environment of the population in the future, we could predict when extinction would occur. Because we can't, we resort to probalistic statements. Limited knowledge of the mean cohort replacement rate because of low sample size is merely an additional source of uncertainty.

A second recommendation for delisting criteria for endangered species in general is the inclusion of some measure of population growth rate as a criterion. This allows the delisting decision to depend on the direct consequences of improvement in quality of the habitat and environment of the listed species. The improvement of natural habitat has been a de facto recommendation associated with almost all listed species, but delisting criteria have typically not

included a specific measure of habitat improvement, except insofar as it might be reflected in current total abundance. Specifying abundance may in some cases adequately reflect habitat quality, but not as specifically and comprehensively as specification of population growth rate. This is particularly important for Pacific salmon and other species that are easily cultured artificially.

There is little special in our choice that the average growth rate be 1.0 (i.e., that the geometric mean of cohort replacement rate be 1.0). It has some appeal due to its deterministic equivalent of a self-sustaining population, but other values could be chosen. Managers should be aware that since the distribution of abundance is lognormal, such a specification only implies that the median population have a growth rate of 1.0; the mode may be less. At some point, the balance between extremely low probabilities of extremely high populations and populations with growth rates less than 1.0 becomes meaningless, and an adaptive approach with close monitoring becomes more reasonable.

One notable, theoretical aspects of the use of a criterion involving population growth rate is the privileged status given to the first few years and the last years used in the estimation of the average growth rate , which in this case is the mean of ln(cohort replacement rate). This effect is strongest and can be most easily seen in the determinate semelparous case, in which estimation of cohort replacement rate involves dividing the number of spawners in one year by the number spawners in the year that would have produced them. In the geometric mean of these, all abundances would cancel, except for the first A years and last A years, where A is the age of maturity. A similar situation arose in the method used for estimating λ developed by Heyde and Cohen (1985), but they found that none of their attempts to incorporate intervening values improved the estimate of the mean.

In summary, we have developed, evaluated and applied a model for viability analysis of the winter run chinook salmon in the Sacramento River. The facts that density-dependence is not important in this species and that it is a single population, rather than a metapopulation, make this stock, and the model, somewhat special. However, it illustrates many of the issues relevant to recovery of the many depleted stocks of Pacific salmon, and at least presents a null case that can provide a context in which to evaluate the more complex situations appropriate for other Pacific salmon.   Some aspects of this formulation may be advantageous for endangered species in general. These include specific accounting for uncertainty in estimating population parameters, and the direct specification of habitat improvement in terms of its effect on population growth rate.

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Table 1. In simulations of winter run chinook salmon beginning at spawning runs of 10,000, the percentage of years in which an extinct cohort increases to above the extinction level, for thresholds of 100 and 50 spawning females.[a]

Spawning age distribution (years)			Threshold abundance	
2	3	4	100	50
0.00	1.00	0.00	0.00%	0.00%
0.01	0.99	0.00	1.66%	1.35%
0.00	0.99	0.01	1.87%	1.38%
0.01	0.98	0.01	1.02%	0.74%
0.10	0.90	0.00	1.15%	0.92%
0.00	0.90	0.10	1.39%	1.12%
0.10	0.80	0.10	0.38%	0.33%
0.00	0.89	0.11	1.40%	1.18%

[a] In all cases mean ln(cohort replacement rate) was adjusted so that the probability of population extinction in 50 years was 0.05.

Figure Legends

Figure 1   A map of northern California showing the former spawning area of Sacramento
               River winter run chinook salmon upstream of the Shasta Dam, the location at
               which adults are counted (Red Bluff Diversion Dam) and the migration path to the
               ocean.

Figure 2   Count of winter run chinook salmon spawners traversing the Red Bluff Diversion
               Dam (solid line), along with the fit to these data used to estimate cohort
               replacement rates. (dashed line). The inset shows the same information on a
               logarithmic scale.

Figure 3   The distribution of the natural logarithms of cohort replacement rates obtained
               from the fit to the spawner counts in Fig. 2. Note that most of the values are less
               than zero, the value corresponding to a constant population in the deterministic
               case.

Figure 4   The modelled effect on age structure on probability of extinction. The increase
               with time in probability of extinction for a semelparous population with spawning
               at age 3, and for similar populations with 1% and 10% spawning at ages 2, 4, and
               both ages. The mean of ln(cohort replacement rate) was -0.2 and the variance was
               1.0. Note the large difference between the semelparous case and the spawning
               distribution estimated for the winter run, 0.89 females at age 3 and 0.11 females at
               age 4.

Figure 5.   Probabilities of extinction within 50 years for the model of the winter run chinook
               salmon for various values of means of the natural logarithms of cohort replacement
               rate and initial population abundance that could be specified in delisting criteria.

Figure 6.   The effect of sampling error on probability of extinction within 50 years for a
               population starting at 10,000 females per spawning run if the geometric mean
               population growth rate is estimated to be 1.0 (i.e., mean ln[cohort replacement
               rate)] estimated to be 0.0) on the basis of a specified number of samples of
               ln(cohort replacement rate) where the standard deviation of ln(cohort replacement
               rate) is 1.0.

Figure 7.   The effect of estimation error on probability of extinction. The probability of
             extinction at various levels of precision in the estimate of spawner abundance [the
             standard error in the estimate of ln(spawners)] for several values of the number of
             samples used to estimate the mean of ln(cohort replacement rate).

Figure 8.   Combinations of parameter values in the recovery criteria that meet the
             requirement that p[extinction]<0.1 in 50 years. These are number of samples of
             cohort replacement rate used to estimate the mean ln(cohort replacement rate), the
             abundance of spawners in a run and the standard error in estimating spawner
             abundance. The values used were nine samples, 10,000 spawners and a SE in
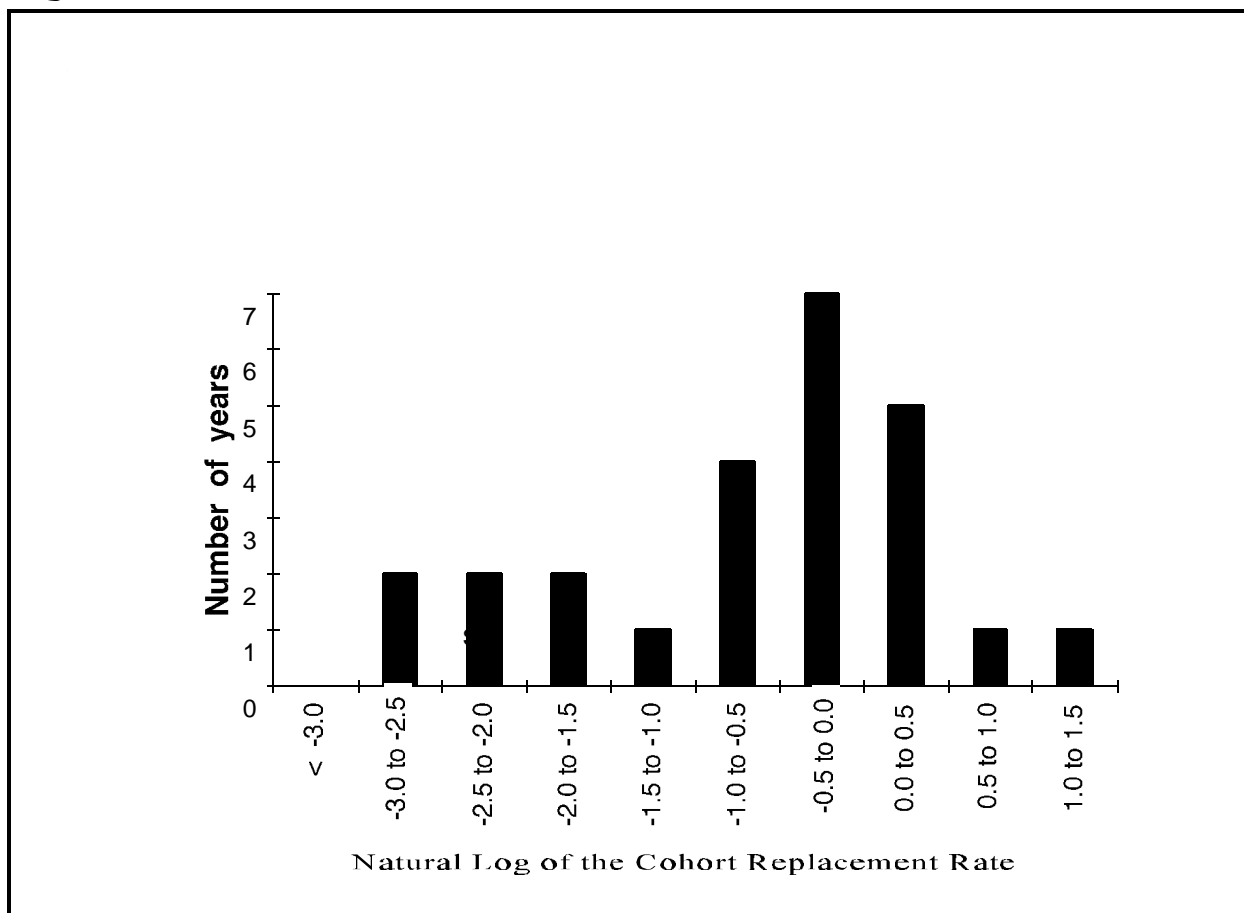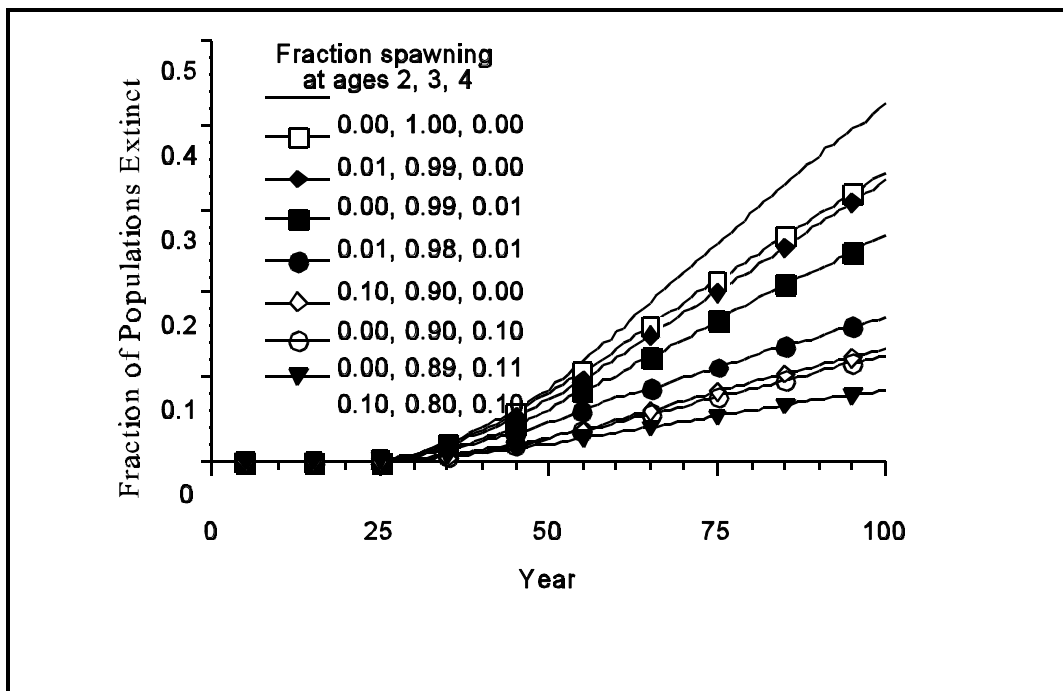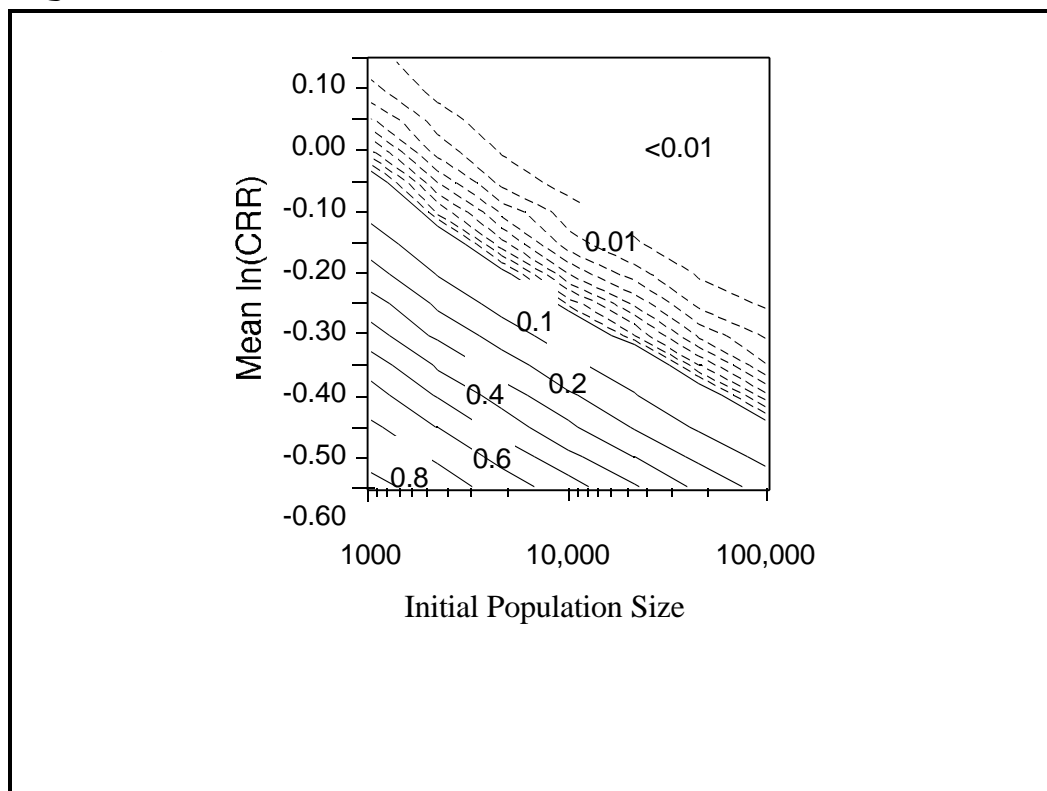   ln(spawners) of 0.25.

Figure 1.
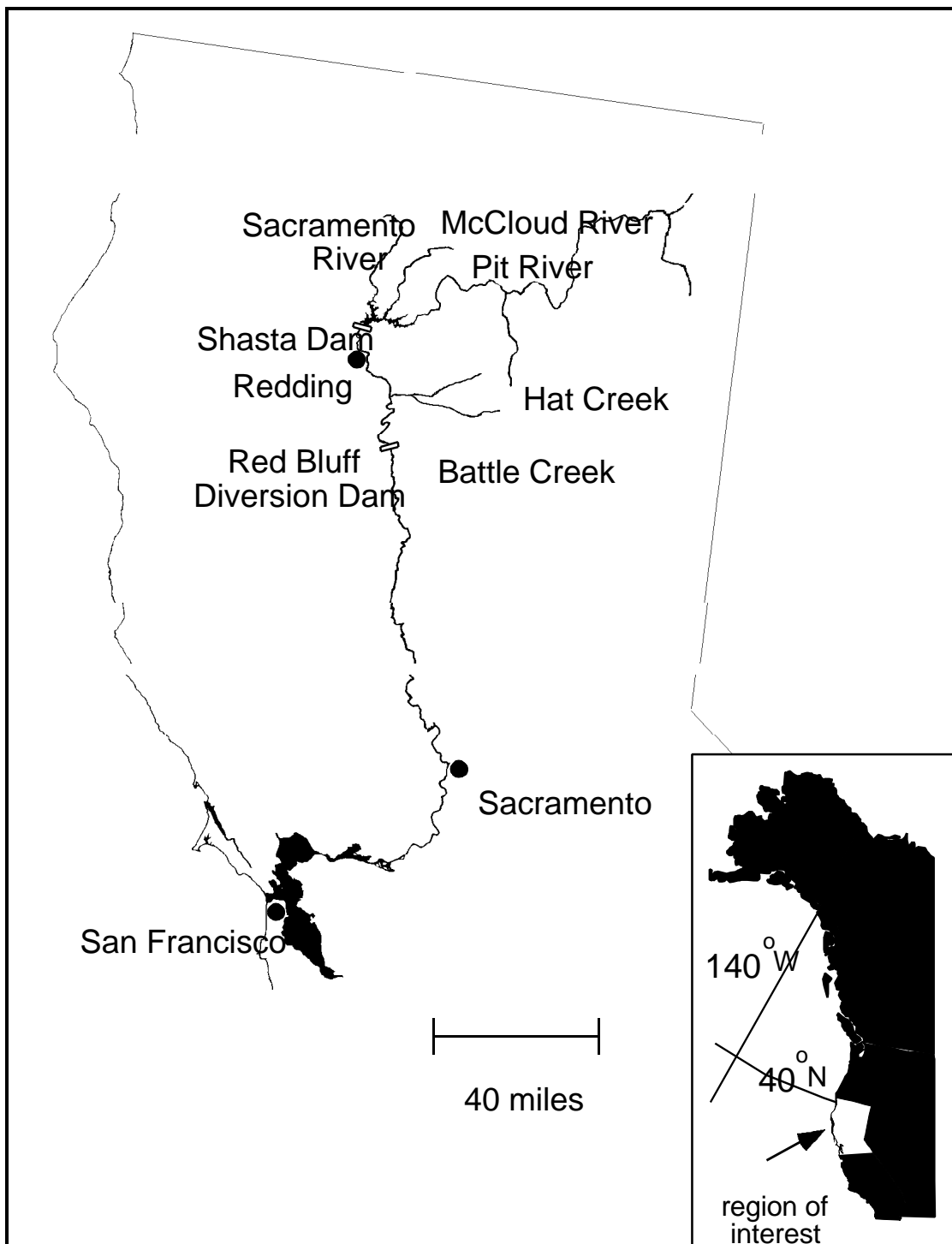
Figure 2.
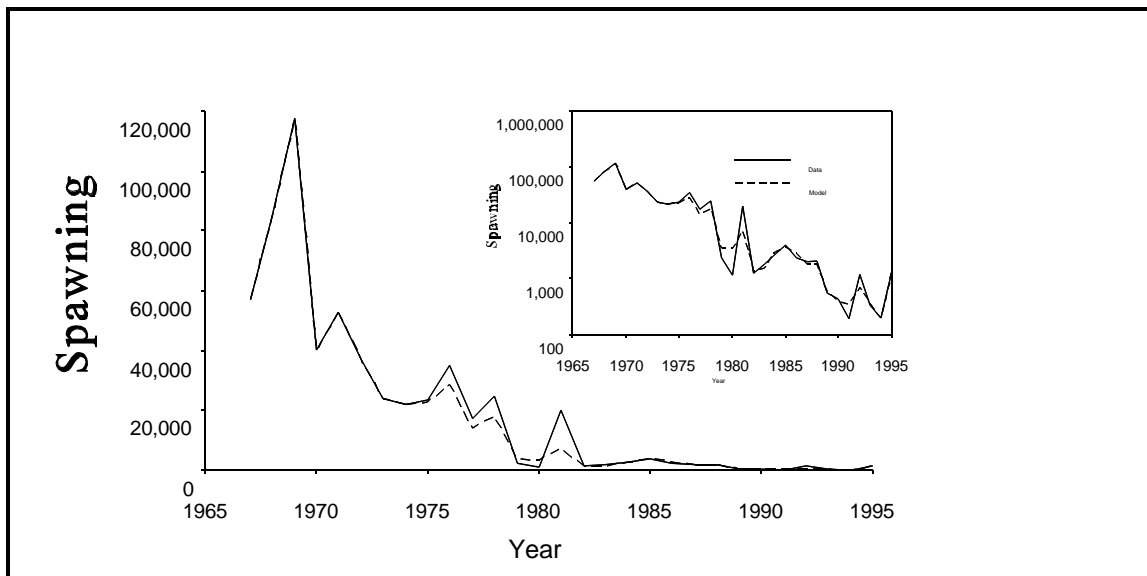
Figure 3.

Figure 4.

Figure 5.

Figure 6.

Figure 7.

Figure 8.